THE EFFECTS OF FOOD DEPRIVATION AND SATIETY ON THE SWIMMING ACTIVITY OF AN AQUATIC COPEPOD, *ORTHOCYCLOPS MODESTUS* (CRUSTACEA: COPEPODA)¹

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(With two text-figures)

Food deprivation for 48 h does not significantly affect the swimming activity of Orthocyclops modestus. Prolonged food deprivation (10 days) results in a significant decrease in activity presumably due to physiological deterioration. Satiety results in an almost immediate cessation of swimming movements which possibly reflects an adaptive mechanism that increases the survival capacity of the species.

One of the most common behavioural responses to food deprivation characteristic of vertebrate animals is an increase in the general level of activity (Bolles 1967; Finger & Mook 1971; Wald & Jackson 1944), coupled with a corresponding increase in willingness to perform certain tasks reinforced by the attainment of food (Beukema 1963; Cofer & Appley 1964; McFarland 1965; Mrosovsky 1964; Smith & Capretta 1956). For example, it has been demonstrated with rats that their rate of performance on an instrumental task (bar pressing) for an equal amount of food reward is inversely proportional to the degree of satiety of the animal (Bolles 1967; Mackintosh 1973; Miller 1955). Previous investigations, although scarce, seem to suggest that invertebrates do not exhibit this direct relationship between the level of hunger and general level of activity (Barton & Evans 1960; Breland & Breland 1966; Marler & Hamilton 1966). The blowfly, Phormia regina, although capable of registering satiety via mechanoreceptors located in the wall of the alimentary canal which

² Department of Biology, Blackburn University, Carlinville, Illinois 62626 (USA). are stimulated by a distension of the gut following feeding, is unable to register degrees of hunger (Dethier 1961; Dethier & Bodenstein 1958; Dethier, Bodenstein & Rhoades 1956: Evans & Browne 1960). As a result, this insect can only discriminate between satiated and non-satiated states, whereas vertebrates can differentiate between various degrees of hunger (Beukema 1963; Bolles 1967; Mackintosh 1973; Prosser & Brown 1961; Tugenhadt 1960). Similar findings have been reported for the cockroach (Reynierse, Manning & Cofferty 1972), and only two additional invertebrates: the amphipods Marinogammarus maand M. obtusatus rinus (Fincham 1972) (Mackintosh 1973; Martin 1966), and the isopod Eurodica pulchra (Jones & Naylor 1970). In view of this fact, the present study was conducted in order to investigate the effects of hunger and satiety on the swimming activity of Orthocyclops modestus (Crustacea: Copepoda), and to then compare these results with those reported for the few species previously mentioned. Information of this nature is not currently available for this group of crustaceans. O. modestus is an aquatic copepod universally distributed throughout the plankton and littoral regions of fresh waters

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(Culver & Brunskill 1969; Elton 1929). Copepods are basically omnivorous, their food consisting of unicellular plant and animal material as well as decaying organic material (Pennak 1953; Wilson 1932).

METHOD

Subjects:

The Ss consisted of adult male Orthocyclops modestus, ranging from 0.7 to 1.2 mm in length. They were collected from a small pond 14 km south of Galena, Stone Co., Missouri. The animals were maintained in constant temperature cabinets at 16°C, and kept on a normal photoperiod regime (12L:12D). They were housed in white porcelain trays containing pond water from the original collecting site, and provided with algae and corn meal daily. The animals were allotted a period of one month to adjust to laboratory conditions before being tested.

Apparatus:

The apparatus consisted of a circular swimming chamber similar to that described by Fincham (1972) and Mackintosh (1973). A glass bowl, 15 cm in diam. and filled to a depth of 5 cm with filtered pond water, was utilized as the swimming chamber. The Ss were introduced individually into the chamber and allowed to swim. Affixed to the bottom of the chamber was a circular paper grid on which were drawn 12 equidistant radii. Swimming activity was measured as the number of line crossings made by an individual in either direction during a given period of time. Water temperature was maintained at a temperature equivalent to that normally encountered by these animals $(18^\circ \pm 1^\circ C)$ by the use of a controlled water bath.

Procedure:

The Ss were divided into two experimental series. The purpose of the first series was to ascertain the effects of food deprivation on swimming activity. Twenty Ss, deprived for 48 h, were tested individually in the swimming chamber (Group 1). Tests with the experimental animals were alternated with tests on a group of 20 normally-fed (non-deprived) Ss serving as controls. A second experimental group of 10 Ss was deprived of food for 10 days and tested in the same way (Group 2), again with alternated tests on 10 non-deprived controls. Swimming activity was recorded over a period of 30 min in 5-min subtotals.

In the second experimental series, the effects of satiation and food deprivation on swimming activity were investigated. Three groups, each consisting of 10 Ss, were tested under the following feeding conditions: normallyfed, 5-day food-deprived, and satiated. Satiation was achieved by allowing the Ss to feed ad lib for 3 h in the swimming chamber prior to testing. Each S was confined in a small plexiglass container and provided with algae and corn meal. The Ss tested under the deprived and normally-fed conditions were also confined for a 3-h period in the absence of food material in order to control against any possible effects of confinement. After this 3-h period, the Ss were removed from the plexiglass holder and their swimming activity was recorded as previously described.

RESULTS

The results of Fig. 1 show that no significant difference was found between the swimming activity of Group 1 animals (48-h deprivation) and the normally-fed controls. However, individuals from Group 2 (10-day deprivation) exhibited a marked decrease in

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Fig. 1. The effects of 48 hr (Group 1) and 10 days (Group 2) food deprivation on the swimming activity of *O. modestus* as compared to that of normally-fed controls.

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Fig. 2. The effects of satiety on the swimming activity of *O. modestus* as compared to deprived (5 days) and normally-fed individuals.

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swimming activity vs. the controls (Mann-Whitney U-Test: z = 4.71; p < 0.01).

From the results shown in Table 1 and Fig. 2 it is evident that satiation reduced swimming activity during the first 15 min. Although the swimming activity between the three groups over a 30-min period did not differ significantly, if the initial 15 min of the experiment are analyzed, values for satiated individuals are significantly below those for the deprived and normally-fed Ss. Observation of the copepods revealed that satiated animals were highly sedentary during this initial period.

DISCUSSION

The results recorded in Fig. 1 show that prolonged food deprivation (Group 2) not only failed to increase general bodily activity, but actually resulted in a significant decrease in swimming behavior. This is in agreement with findings reported for amphipods (Fincham 1972; Mackintosh 1973). Since this deprivation effect increased with time it can presumably be attributed to some physiological deficiency. Group 1 Ss, deprived for a period of time of insufficient duration to cause physiological deterioration (48 h), exhibited no significant difference in swimming activity over that demonstrated by the controls. This is further substantiated by the results shown in Fig. 2 for Ss deprived for 5 days, also a period of time insufficient to cause physiological deterioration (Pennak 1953). It can be concluded therefore, that within the limits of physiological tolerance, food deprivation does not result in an increase in bodily activity for O. modestus. This is in direct contrast to the response of vertebrates which is characterized by a significant increase in the general level of activity within physiological limits of tolerance (Barton & Evans 1960; Bolles 1967;

Finger & Mook 1971; Marler & Hamilton 1966). It is evident therefore, that the behavioural responses to hunger exhibited by some invertebrates are very different from those charactristic of vertebrate animals. Future investigations on many invertebrate species should be undertaken in order to further substantiate this conclusion.

The results in Table 1 and Fig. 2 show that satiated individuals were characterized by an initial significant decrease in swimming activity. However, in this case, the inhibition of activity appears to be due to a modification of behaviour rather than to any physiological deterioration since activity increased after the first 15 min. It is possible that this intial decrease in mobility is indicative of a more general adaptive mechanism. Barton & Evans (1960) have reported that blowflies which have never previously been fed exhibit spontaneous locomotor activity; this activity is markedly reduced immediately after feeding. This has also been verified for locusts (Ellis & Hoyle 1954) and amphipods (Mackintosh 1973). It is well known that hunger induces exploratory and foraging behaviour in animals (Campbell & Sheffield 1953: Fowler 1965; McFarland 1965; Mrosovsky 1964) which ultimately terminates in a consummatory response (Bolles 1967; Cofer & Appley 1964). However, once an organism has fed and foodseeking behaviour is no longer necessary, the survivability of the organism is increased if locomotion is inhibited. Any mechanism which reduces activity thereby rendering the animal less conspicuous to potential predators, is of important adaptive significance. O. modestus responds to satiation by an immediate drastic reduction in swimming activity. Since copepods are a potential food source for numerous aquatic predators, such an immobilization would effectively decrease the level of

predation and as a result increase the survival capacity of the species. Unlike the hunger response, with respect to satiety *O. mode*-

stus exhibits a decrease in activity similar to that found in vertebrates.

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